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Edaphic and bathymetric segregation of the spider crab, Chionoecetes opilio (O. Fabr.), in the southwestern Gulf of St Lawrence[1]

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Coulombe, F., J.-C. F. Brêthes, R. Bouchard et G. Desrosiers. 1985. Ségrégation édaphique et bathymétrique chez le crabe des neiges, *Chionoecetes opilio* (O. Fabr.), dans le sud-ouest du golfe du Saint-Laurent. Can. J. Fish. Aquat. Sci. 42: 169–180.

Des observations sur une population de *Chionoecetes opilio* ont été effectuées au cours des été 1980 et 1981 dans le sud-ouest du golfe du Saint-Laurent, à l'entrée de la baie des Chaleurs et de la baie de Gaspé. L'échantillonnage a été réalisé à l'aide d'un chalut à perche et de casiers appâtés, à des profondeurs variant de 45 à 125 m. Les largeurs de carapace des crabes des deux sexes ont été mesurées et la maturité physiologique déterminée par indice biométrique. Les individus prématures des deux sexes se distribuent préférentiellement aux niveaux bathymétriques supérieurs sur des substrats hétérogènes gravelovaseux tandis que les adultes sont rencontrés surtout en profondeur sur les fonds de vase et de vase sableuse. On émet l'hypothèse que les jeunes crabes descendent vers les fonds de vase où se produit le recrutement à la pêche. Ce déplacement serait concomittant à l'apparition de la maturité physiologique.

A population of *Chionoecetes opilio* was studied during the summers of 1980 and 1981 in the southwestern Gulf of St. Lawrence, at the entrance of the Bay of Chaleur, and the Gaspé Bay. Sampling was conducted with beam trawls and baited traps at depths ranging from 45 to 125 m. Crab shell width of both sexes was measured and physiological maturity determined according to a biometrical index. Immature individuals of both sexes are essentially localized on the upper bathymetrical levels, on gravelly mud, whereas adults are found mainly on mud or sandy mud bottoms. We hypothesize that young crabs move down to the muddy bottom where recruitment to the fishery occurs. This deplacement seems to be concomitant with physiological maturity.

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The species Chionoecetes opilio (O. Fabr.) is common in the Gulf of St Lawrence, where it is commercially exploited. The spider crab's usual habitat is in muddy areas in deep water (Brunel 1960), but it can also be found on firmer bottoms (Powles 1968). Similar studies by Ledoyer (1975) and Miller (1975), performed at the entrance to the Bay of Chaleur and Gaspé Bay, have shown concentrations of small crabs at shallow depths on gravelly or rocky bottoms. In subsequent exploratory fishing operations using commercial fishing gear, Miller and O'Keefe (1981) observe an increase in crab size with depth in Newfoundland's Conception Bay.

It is therefore hypothesized that the various elements of the spider crab population (males, females, matures, immatures) are not randomly distributed within a single habitat but that a certain segregation exists, relating to such ecological factors as bathymetry and sediment granulometry. The purpose of this study, which was performed during the summers of 1980 and 1981, in the southwestern Gulf of St Lawrence, is to confirm the bathymetric distribution of the species C. opilio and to assess the influence of the nature of the substrate on this distribution.

Description of the study area

The study area is located in the southwestern Gulf of St Lawrence, between 64°00' and 64°30' W and between 48°10' and 48°50' N. It includes the entrance to the Bay of Chaleur, Malbaie and the entrance to Gaspé Bay (fig 1), an area of approximately 2500 km^2. The sedimentology of this sector has been studied by Brunel (1970), Loring and Nota (1973), Ledoyer (1975) and Coulombe (1983). Four sedimentological zones can be defined (fig 2): pure muds, sandy muds, muddy sands and pelitic gravels.

The pure mud zone lies essentially along the axis of the Bay of Chaleur, at depths of generally more than 90 m. The pelitic content of these sediments is rarely less than 95%; the remaining fraction consists of very fine sand. Pure muds are also found in Gaspé Bay, beyond the 75 m isobath.

The sandy mud zone occupies a more limited area. It forms a transition zone between the pure muds and muddy sands on either side of the

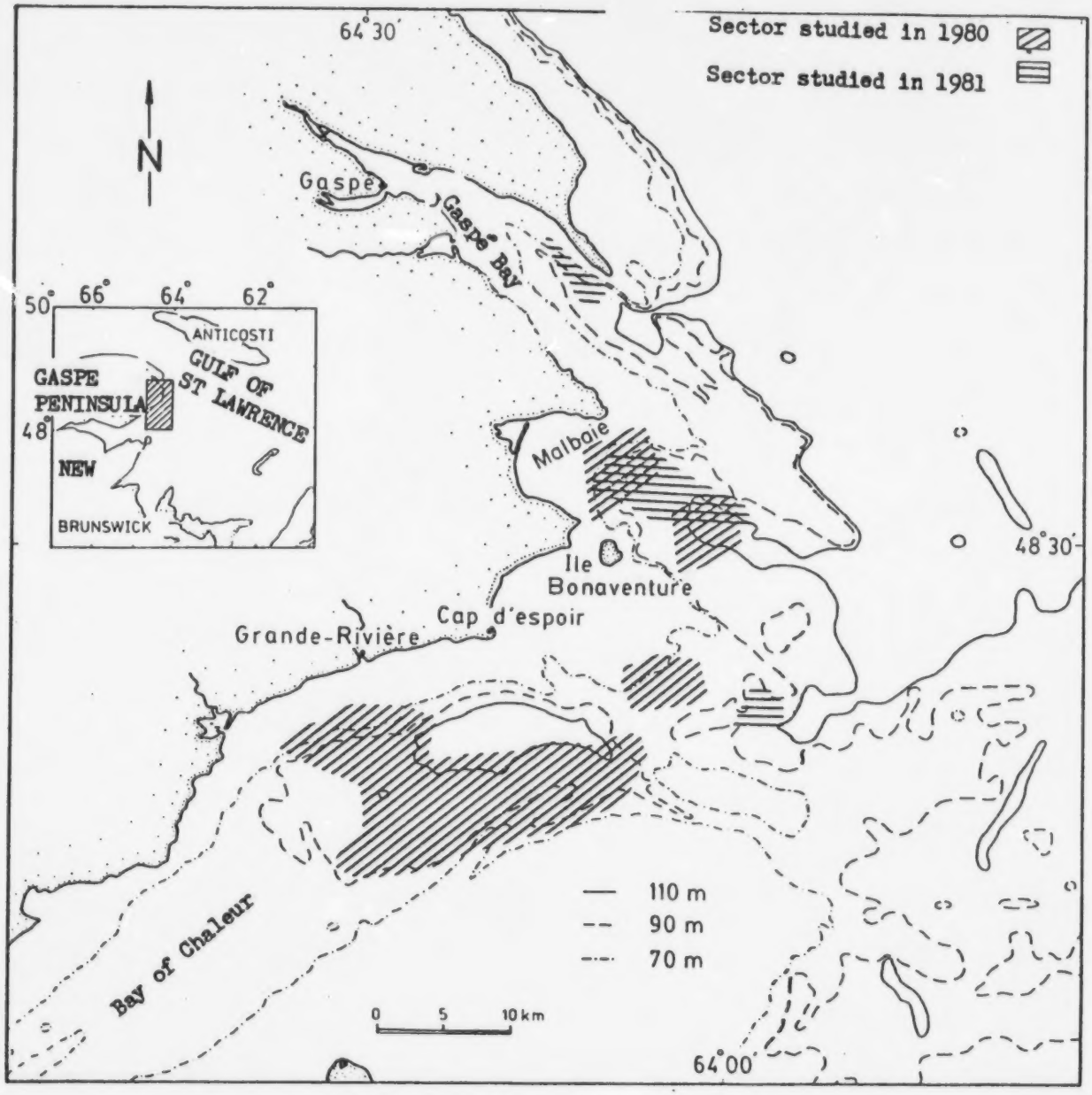

FIG 1. Location of the study site

Bay of Chaleur channel at depths ranging between 75 and 90 m. It extends across the mouth of Malbaie, where it is juxtaposed to muddy sands. It occurs

at depths of between 70 and 120 m. It may be noted that pure muds occur at similar depths in the Bay of Chaleur. Pelites account for 60 to 80% of the content of the samples. Sandy muds surround the mud zone in Gaspé Bay.

In terms of area, muddy sands represent one of the two major zones of the sector studied, the other being the pure muds. These muddy sands are located essentially around the muddy zones of the Bay of Chaleur and at the entrance to Malbaie. They occur at depths of between 35 and 75 m. Their composition varies and is strongly influenced by the proximity of the other sedimentary zones.

Lastly, the pelitic gravel zone is thinly distributed through the sector; from west to east, it occurs along the Gaspé coast, off Cap d'Espoir, on the north-south axis of Ile Bonaventure, and in the centre of Malbaie. A final area lies off the southeast coast of Ile Bonaventure. It extends generally from 20 to 35 m, although under certain conditions it may go as deep as 75 m. It is characterized by a preponderance of gravels and pebbles, consolidated by finer elements.

Hydrological studies by Lauzier et al (1957) and by Lauzier and Bailey (1957) have shown that, at approximately the 30 m level, a thermocline tends to develop between the surface waters, which show wide thermal fluctuations, and an intermediate layer, in which temperatures vary little over the year (-1 to 2°C). The deep-water stratum encountered between 200 and 300 m in the

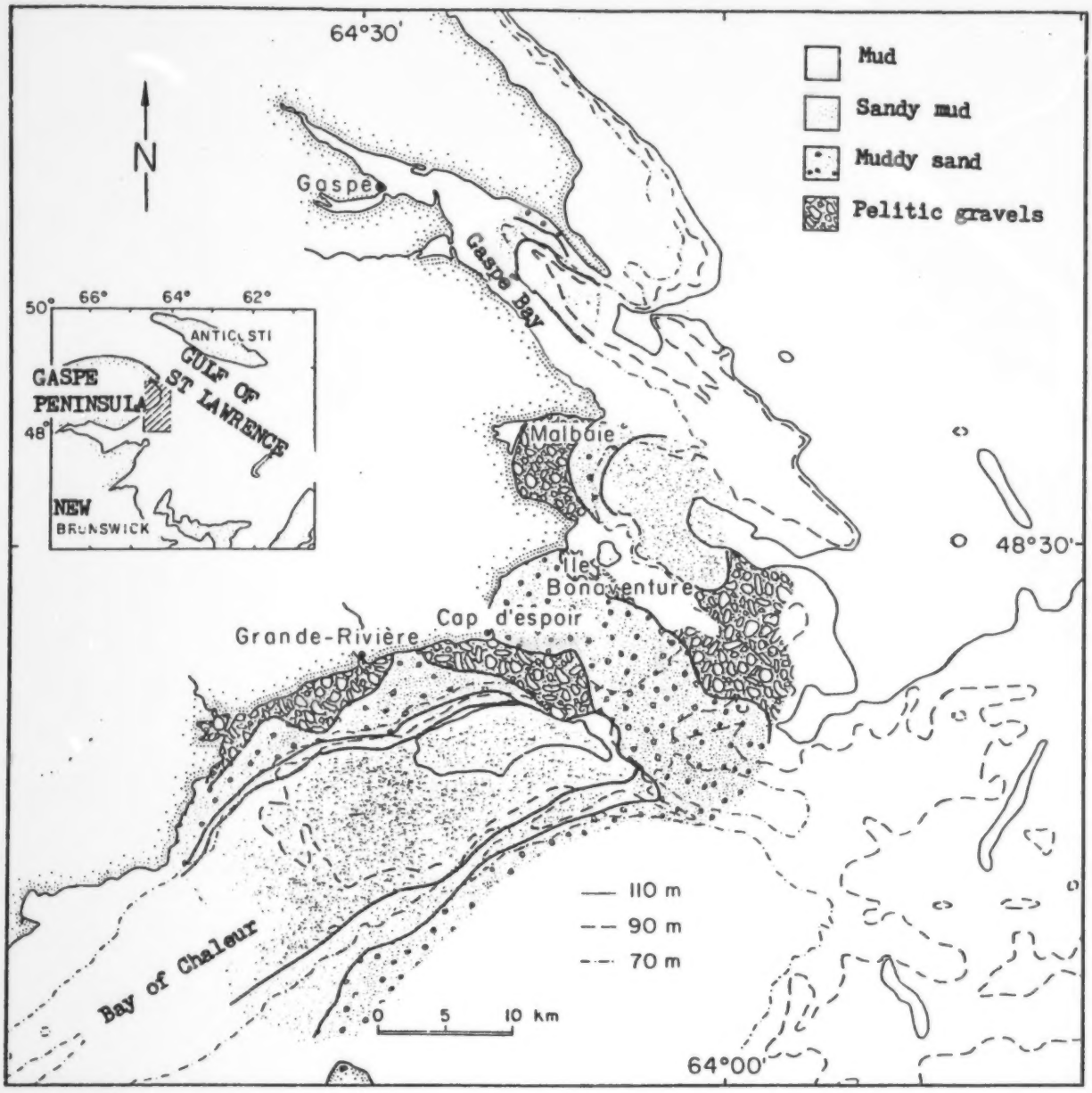

FIG 2. Distribution of the principal types of substrate

Gulf of St Lawrence is absent, since the Bay of Chaleur has a maximum depth of 180 m (Loring and Nota 1973). According to Brunel (1970), then, we have: the surface waters, of variable temperature and low salinity (25-31‰) and the

very cold intermediate waters, with average temperatures of around 0°C and higher salinity (31 to 33‰).

Coulombe (1983) has proceeded further with the studies performed by Brunel (1970), Ledoyer (1975) and Bellan (1978) on the structure of the benthic invertebrate populations. One population is associated with extremely muddy bottoms and corresponds to that typical of muds in arctic waters (Ledoyer 1975) or the arctic community of cohesive muds (Brunel 1970), which is comparable to the community of the polychaete Maldane sarsi and the ophiuroid Ophiura sarsi (Coulombe 1983). The heterogeneous bottoms with which we are concerned (muddy sands and pelitic gravels) are occupied by the population typical of muddy sands in arctic waters (Ledoyer 1975) or the subarctic muddy sands community (Brunel 1970), which is comparable to the bivalve Macoma calcarea community (Coulombe 1983). The spider crab, C. opilio, belongs to both of these communities, although it has been considered primarily a member of the mud-dwelling community (Brunel 1970).

Materials and methods

Samples were taken in May and September 1980 at the entrance to the Bay of Chaleur and in Malbaie; in 1981, the Malbaie sector was visited in May, July and September, and Gaspé Bay in May. The depths ranged from 45 to 125 m.

TABLE 1. Summary of sampling performed in 1980 and 1981 for spider crab C. opilio. Substrate: MH = muddy heterogeneous bootoms; SM = sandy mud; M = mud. Gear: T = trawl; BT = baited trap.

Date	Location	Depth (m)	Substrate	Gear	Number of tows or hauls
May 1980	Malbaie	80-90	MH	T	4
		90	MH	T	3
		100	SM	T	2
		110	SM	T	7
	Bay of Chaleur	75	MH	T + BT	2 + 2
		80-90	MH	T	1
		80-90	SM	T	1
		90-100	SM	T	4
		90-100	M	T	1
		100+	SM	T	1
		110+	M	T	4
Sept 1980	Malbaie	80-90	MH	BT	3
		90-100	MH	BT	2
		100-110	SM	BT	5
	Bay of Chaleur	110+	M	BT	3
May 1981	Gaspé	70	SM	BT	12
		80-90	SM	BT	12
		90-100	M	BT	24
		125	M	BT	12
		80-90	MH	BT	24
		90-100	SM	BT	12
July 1981	Malbaie	40-70	MH	BT	24
		80-90	MH	BT	12
		100	SM	BT	12
Sept 1981	Malbaie	60	MH	BT	12
		75	MH	BT	12
		90	MH	BT	12
		110	MH	BT	12

The crabs were caught by means of two different techniques. In May 1980, 51 trawl tows, of 30 min each, were performed in the Bay of Chaleur and Malbaie between sunset and sunrise. The small beam trawl used had a 1.80 m horizontal opening and was lined with 25-mm mesh webbing (stretch measure). This was subsequently replaced by Japanese-style conical traps, mesh size 45 mm (stretch measure), set on groundlines. In 1981, flat traps were also used to improve the probability of catching small crabs. No significant difference was observed between catches with the two types of traps (R Bouchard, unpublished data) and they were therefore considered comparable. The traps were baited with approximately 1.5 kg of frozen herring and left in position for a period of approximately 24 hr. The results of the sampling are summarized in table 1.

Crab size is indicated by maximum carapace width, measured to the nearest millimetre. Physiological maturity was estimated on the basis of biometrical measurements: the width of the chela for males and the width of abdominal segment 5 for females. This method has the advantage of being very rapid and non-destructive. According to Watson's data (1970), a male is considered mature when the ratio of chela width to carapace width is equal to or greater than 0.19, and a female when the ratio of abdomen width to carapace width is equal to or greater than 0.55.

In order to test the validity of the method used, male chela width was plotted against carapace width (fig 3): two clouds of points can be distinguished, more or less clearly divided by the line Wch = 0.19 Wca. In addition, we compared the curve of appearance of maturity obtained by biometrical measurement (fig 4) with that obtained by Watson (1970) from observations of the genital tract. According to the biometrical method, 50%

of the males are mature at 62 mm carapace width, compared to the 57 mm obtained by Watson. For females, the threshold is identical, at 50 mm. The biometrical method appears to overestimate the proportion of immature males in the population, but seems to be precise enough for the purposes of this study.

The bathymetric gradient was divided into five depth levels: under 80 m, 80 m to under 90 m, 90 m to under 100 m, 100 m to under 110 m, 110 m or more. In addition, we used three substrate categories: muds, sandy muds and muddy heterogeneous bottoms, the latter including muddy sands and pelitic gravels. We compared the distribution of immatures on the basis of these parameters, using two non-parametric tests, the Mann-Whitney U test and the Kruskal-Wallis K test. The effect of the two ecological parameters

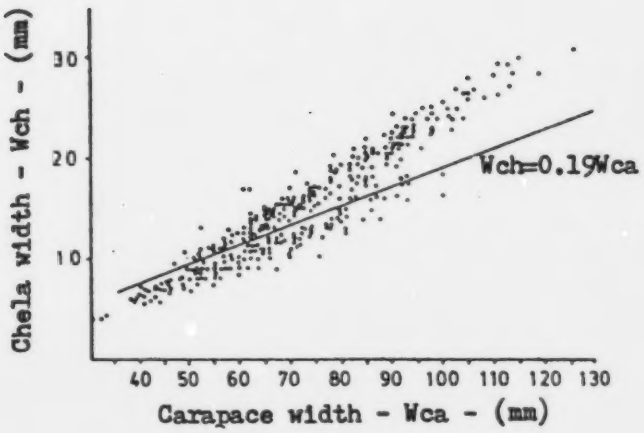

FIG 3. Relationship between chela width and carapace width in C. opilio males

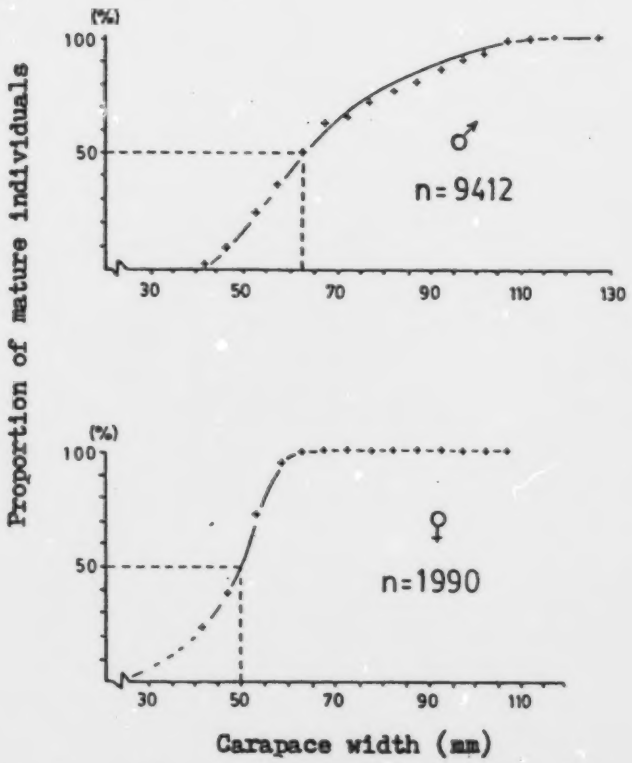

FIG 4. Curves of appearance of physiological maturity obtained by the biometrical index

on size frequency distributions was studied by correspondence analysis (Benzecri et al, 1980). This technique is applicable to contingency tables and, more generally, to tables of data consisting of positive or zero-value integers.

The purpose of the analysis is to identify the "best" simultaneous representation of the observation points and variable points in a common system of orthogonal axes. The distance between two observations, or two variables, is given by the chi-square metric. The interpretation is based, in this case, on study of the plane projection of the clouds of observations and variables. These variables are carapace widths, grouped in 5 mm classes, expressed in parts per thousand. The percentage of immatures was introduced as a supplementary variable; this factor thus does not affect the general image of the projection, but its position assists in clarifying the interpretation. The observations do not correspond, here, to the samples taken but to the eight ecological variables (five bathymetric levels and three substrates) for the five sampling periods. Each entry in the matrix thus corresponds to the proportion of individuals of a given size on a given type of substrate, or at a given depth, at a given period. The computer program used is that described by Lebart and Fénelon (1975).

Results

Distribution of males

The size frequency distributions (fig 5 and 6) are distributed around a mode at 65-77 mm present in all the samples, regardless of period, region or depth. At depths of less than 90 m, the distributions show a higher proportion of small sizes, and we note a secondary mode at 45 or 50 mm. In

the deeper zones, beyond 90 mm, the large sizes predominate, and the secondary mode occurs at about 85-90 mm carapace width. This pattern is coherent within each region and period. The 45 mm mode, however, appears only in 1980 (fig 5) and in May 1981 in Malbaie (fig 6A). One exception appears to be the series of samples taken in July 1981 (fig 6C), in which few differences are observed between the two depth levels represented.

If we look at the percentage of immature males in the samples, we see that it declines with increases in depth, on the one hand, and with increases in the fine fraction of the sediment, on the other (fig 7). On the basis of bathymetry, bottoms at less than 80 m support an average of 61% (±21%) immatures, those at 80 to 90 m 65% (±18%), those at 90 to 100 m 46% (±17%), those at 100 to 110 m 29% (±13%) and those at the deepest levels 12% (±13%). Classified on the basis of substrate granulometry, muddy heterogeneous bottoms show 65% (±11%), sandy muds 22% (±8%) and pure muds 36% (±16%). Kruskal-Wallis rank variance analysis of the samples from heterogeneous bottoms shows that bathymetry plays no significant role when the immatures are located on this type of substrate ($\underline{K} = 0.2$; $\underline{K}_{(2-0.05)} = 6.0$). On sandy mud, in contrast, there is a significant decline in the proportion of jeveniles with increases in depth ($\underline{K} = 12.8$; $\underline{K}_{(2-0.01)} = 9.2$). If we look at all levels where heterogeneous bottoms or sandy muds occur at less than 100 m, the Mann-Whitney $\underline{U}$ test indicates that, on average, immatures are better represented on the first type of substrate, with 65%, than on the second, with 40% ($\underline{U} = 38$; $\underline{U}_{0.05} = 38$). Finally, there is no significant difference between muds and sandy muds for depths of 100 m or more.

In order to interpret the results of correspondence analysis, we have represented the projection of the size classes, on the one hand, and that of the mean position of each ecological variable, on the other, in the factorial plane formed by the first two axes (fig 8). We note a very

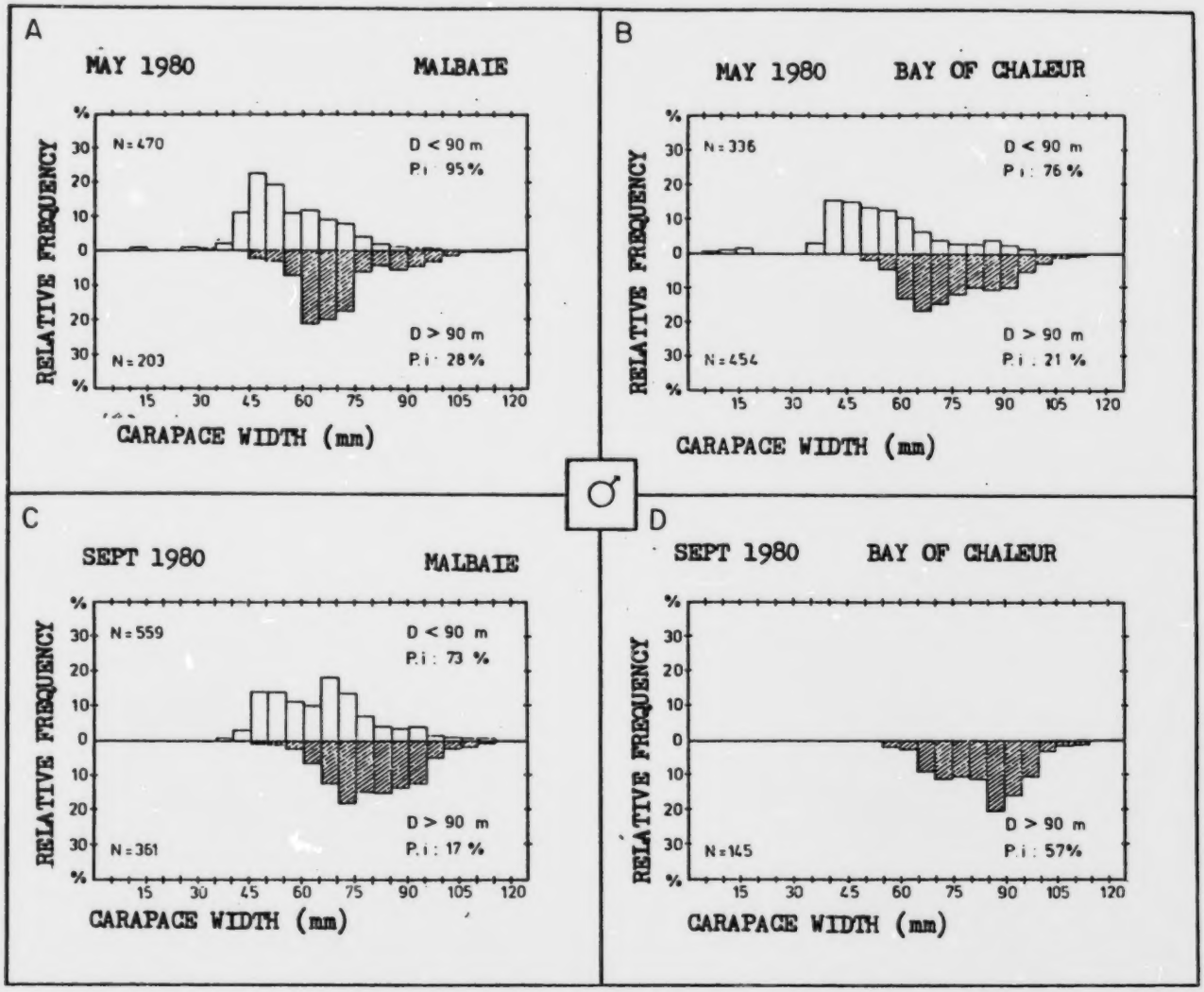

FIG 5. Size frequency distribution of C. opilio males collected in 1980 (D = depth; Pi = percentage of immatures; N = number of individuals)

clear arrangement along axis 1, which alone explains 71% of the variability in the data, as compared to 10% for axis 2; this reflects the relatively marked correlation between granulometry and bathymetry and also between size classes and ecological variables. There is thus a segregation of sizes associated with the nature of the substrate and the depth. On the negative abscissa we find the smaller size classes (55 mm or less) associated with

depths of less than 90 m and heterogeneous substrates. The supplementary variable, the percentage of immatures, appears to be related to this group. It is opposed, on the first axis, to the larger class sizes (80 mm or more), which are associated with the finer substrates and greater depths, 100 and 110 m. The 90 m stratum lies at the transition, near the origin of the axes; the 60 mm size class occurs in the same position for all carapace widths.

The variation of this image over time is given by the projection on the first axis of the ecological variables for each of the sampling periods (fig 9). The average pattern shown in fig 8 does not appear constant in time. Segregation on the basis of bathymetry and substrate is clearly apparent in May 1980 and September 1980, although different gear was involved. It is still evident in May 1981. The proximity of shallow levels to finer granulometry at this testing period is due to the samples taken in Gaspé Bay. The segregation becomes less distinct in July and September 1981, with greater homogeneity of the population between the various depths and substrates.

Distribution of females

The location of the females does not appear to follow the same pattern. They are relatively scarce at the shallowest levels and much more abundant at the deepest levels. This observation may, however, reflect a distortion introduced by the use of traps, since the trawling performed in May 1980 collected significant quantities of female crabs at depths of 85 m. The size of the mesh used in the traps appears to result in an underestimation of the size frequency distribution of the smallest individuals, those under 45 mm. These samples thus reflect a distorted image of female size

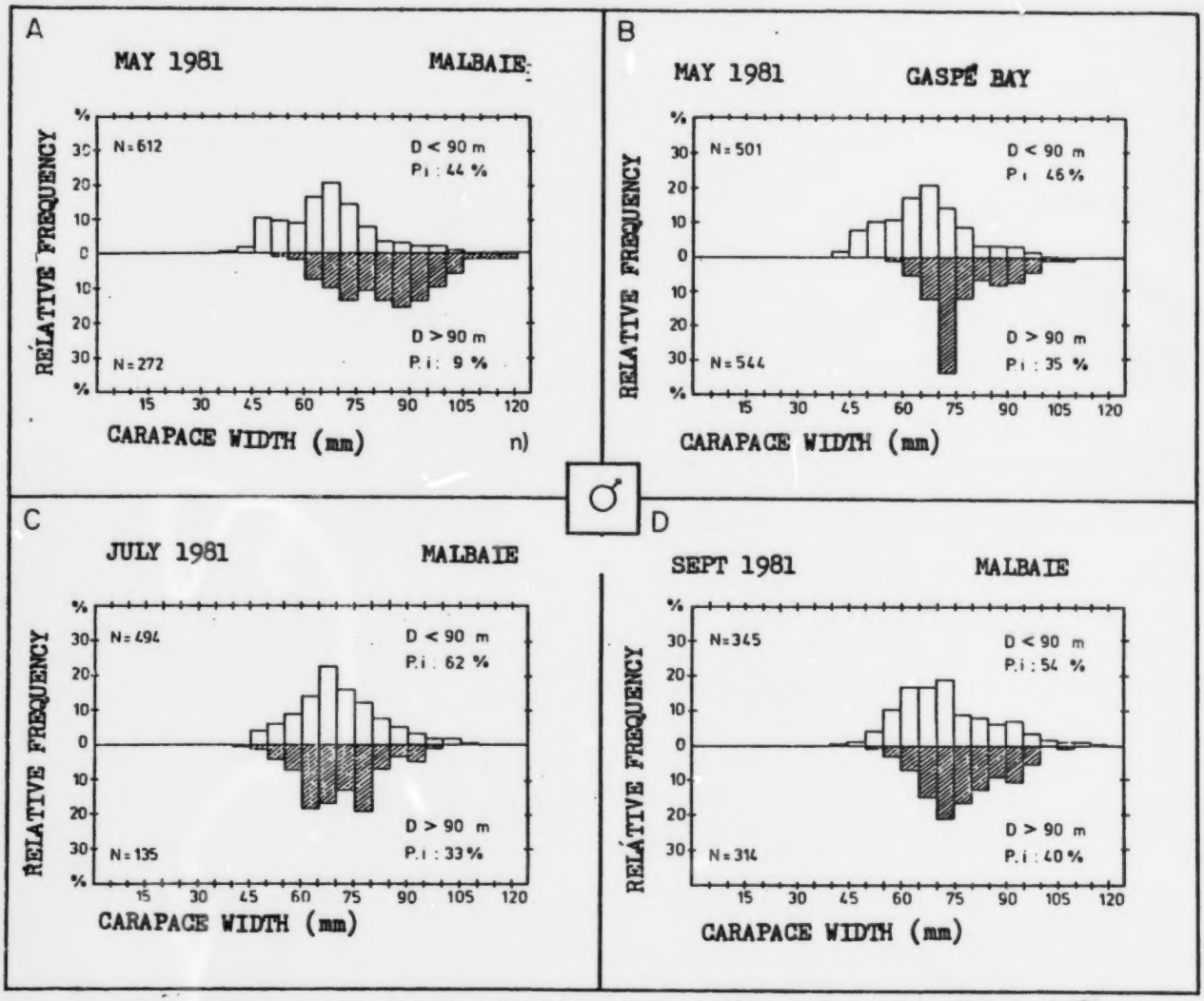

FIG 6. Size frequency distribution of C. opilio males collected in 1981 (same legend as fig 5)

distribution in the environment. Some idea of this distribution can be obtained, however, from the samples collected in 1980 (fig 10). As with the males, we observe a certain increase in size with depth, one mode at 45-50 mm being noted on bottoms of less than 90 m and a second, around 65 mm, in deep water. The distribution of immature females follows this pattern as well, at

least in 1980; we find 21% immature females on bottoms of less than 90 m in Malbaie in May (fig 10A) and 60% in the Bay of Chaleur, at the same period and the same depths (fig 10B). In September of the same year, we again note 66% immature females on bottoms of less than 90 m in Malbaie (fig 10D), despite the fact that these samples were collected by means of traps. In 1981, the proportion of immatures caught remained constant at around 10%.

Ratio of the sexes

The mean ratios between the sexes, in terms of percentages of males observed in the samples (fig 11), show a tendency to an increase in the proportion of females with depth. In May, both in 1980 and in 1981, this proportion varies widely from one sample to another, possibly indicating a distribution in clusters consisting of either males or females. This ratio between the sexes shows a seasonal variation. While adult females appear relatively well represented at all depths at the beginning of the season, in the fall they are found almost exclusively in deep water.

Discussion

Bathymetric and edaphic segregation

Crustacea Decapoda are frequently observed distributed along a bathymetric gradient on the basis of size. This is true, for example, of the crab Cancer pagurus in the English Channel (Brown and Bennett 1980), of the spiny lobster of the Palinuridae family (Kanciruk 1980) and of the European lobster, Homarus gammarus, although in this species the nature of the substrate plays a role, separating adults and juveniles at the same bathymetric level (Howard 1980). In a distinctly vasicolous species such as

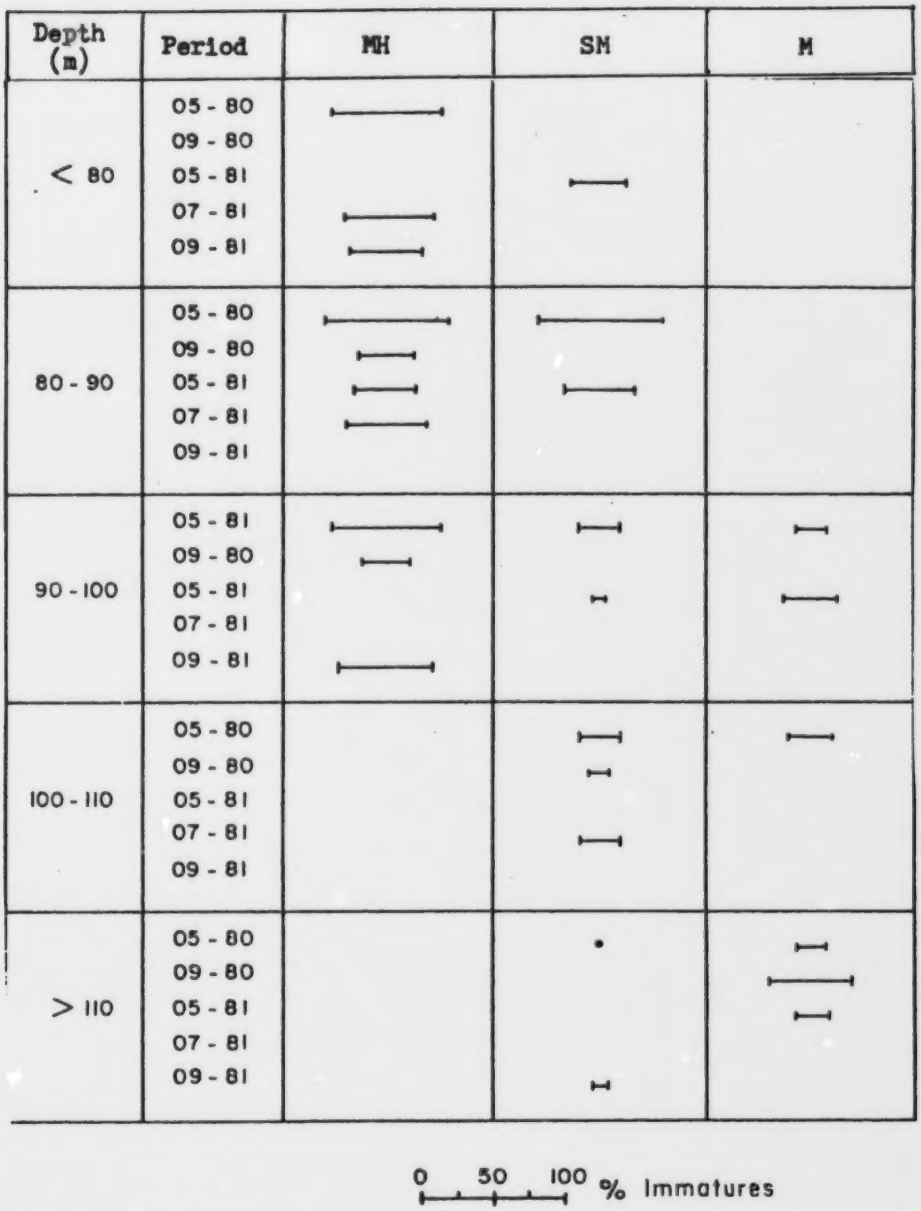

FIG 7. Percentage of immature males by bathymetry and substrate, all regions combined (MH = muddy heterogeneous bottom; SM = sandy mud; M = mud)

the Norway lobster, Nephrops norvegicus, depth plays no role (Chapman 1980). In C. opilio, the increase in size with depth had already been noted by Miller and O'Keefe (1981) in Newfoundland's Conception Bay, but the

fishing gear used provided no information on juveniles. Here again, then, bathymetry appears to be a determining factor in the distribution of the spider crab population, since we observe both an increase in size and a reduction in the representation of juveniles with depth. It appears, however, that granulometry is also an important factor in disrupting the monotony of the bathymetric distribution of this species.

Interpretation of our data may, however, be distorted by our sampling methods. Very heterogeneous bottoms are not suitable for trawling and the mesh used on the traps is too large to retain individuals < 45mm, thus explaining the limited number of immature females collected by this means. In addition, the image of the population varies with the fishing technique used. The trawl appears to have been effective in collecting small individuals; for example, crabs of carapace width < 30 mm were caught in May 1980 (fig 5B). However, it appears to underrepresent the larger crabs, which, because of their mobility, are able to evade this type of gear. In the traps, in contrast, the large sizes are much better represented, while the smaller individuals can escape through the mesh. This explains the fact that, in the results of correspondence analysis (fig 9), the samples taken in

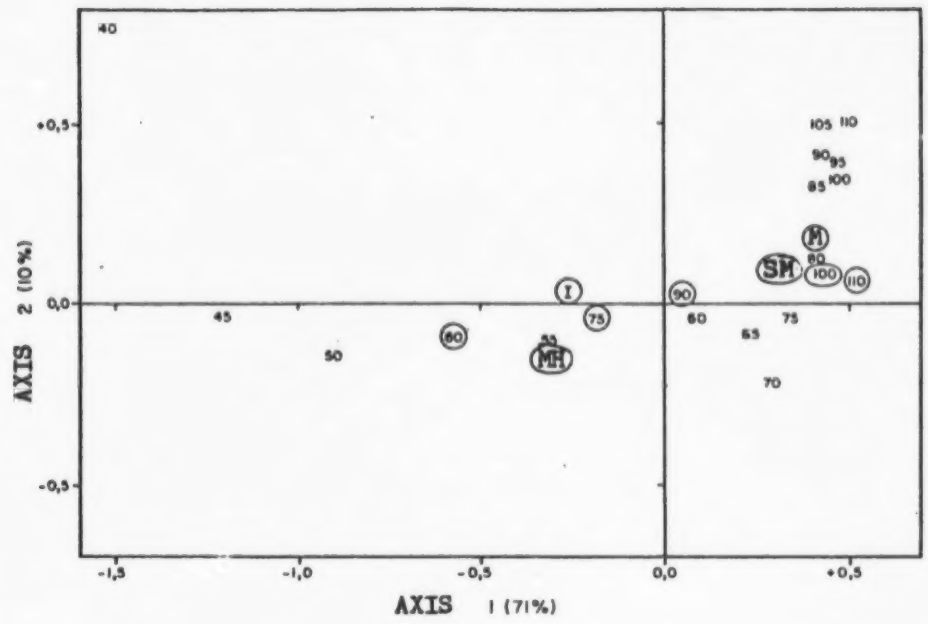

FIG 8. Correspondence analysis of male distributions. Plane projection of size classes (uncircled figures) and mean positions of ecological parameters: bathymetric level and sediment classes (circled figures) (MH = muddy heterogeneous; SM = sandy mud; M = mud; I = percentage of immatures introduced as a supplementary variable).

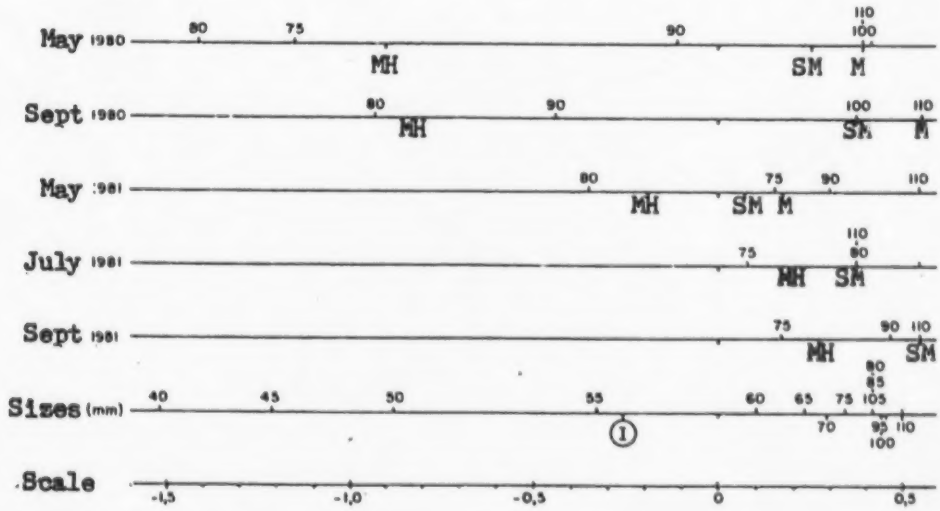

FIG 9. Correspondence analysis of male distributions. Projection of size classes and ecological parameters, for each sampling period, on the first factorial axis (same legend as fig 8).

May 1980 on bottoms of less than 90 m show a closer relationship to small male sizes (under 55 mm) than the other samples. We can thus explain the high proportion of immature females found at this time. We note, however, that the data collected on traps in September 1980, while overrepresenting the larger sizes, give a pattern very similar to that observed in May (fig 5A, 5C and 9). It is quite probable, then, that the variations observed are associated more with variations in the population sampled than with distortions related to the type of gear used.

In the segregation observed, it is difficult to separate the influence of the bathymetric gradient from that of granulometry, since the two factors are closely correlated. We observe, however, that the increase in depth does not play a major role in the distribution of juveniles located on heterogeneous bottoms, which support a higher proportion of immatures than the other substrates. It thus appears that young, immature males, 45 to 55 mm, prefer this type of habitat. It is reasonable to assume that the coarse elements of the substrate serve to shelter the young crabs from their predators. Following metamorphosis, young C. opilio are subject to

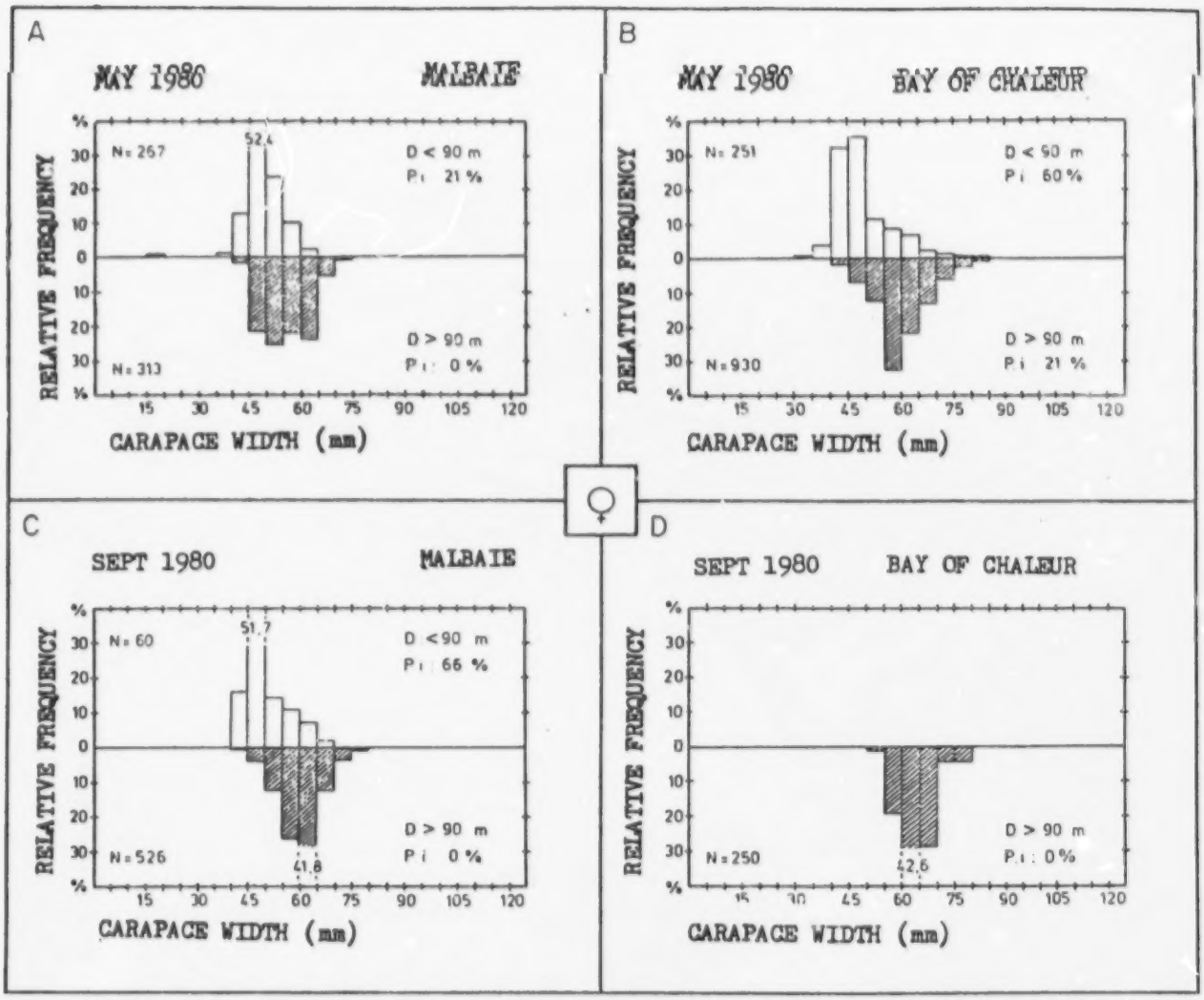

FIG 10. Size frequency distribution of C. opilio females collected in 1980 (same legend as fig 5).

intense predation (Bailey 1982; Waiwood and Elner 1982) and those located on heterogeneous substrates could thus achieve a higher survival rate.

The first factorial axis in the correspondence analysis appears to arrange male size classes by their degree of sexual maturity: at one end we find totally immature individuals, associated with heterogeneous bottoms, and at the other, totally mature individuals (80 mm or more) associated with finer

granulometries (fig 8). Between the two fall all those individuals which may be one or the other, in positions intermediate between the various substrates and bathymetric levels. The 60 mm size, at which 50% of the males are physiologically mature, occurs at the midpoint, close to the origin of the axes, near the 90 m depth, at which all three types of substrate may be found and which appears to be a true transition zone. Over the life cycle of C. opilio, there thus appears to be a progressive change in habitat, from heterogeneous bottoms to muddier bottoms, a change concomitant with the appearance of physiological maturity. This observation seems to have been verified for males, but only the 1980 data support a similar hypothesis for females.

Study of the sex ratio indicated clear dominance of the females in deep water. This situation appears to be related to fishing activities, which are directed exclusively towards large males and performed primarily on these types of bottoms. One final observation, the reduction in the proportion of adult females between May and September at the upper bathymetric levels (figure 11), would appear to suggest that they leave these levels during the summer.

Recruitment mechanism

The general pattern of distribution of C. opilia which we have described suggests that individuals move to the deeper and muddier zones in relation to the moult cycle. For females, the moult of puberty occurs immediately prior to mating, which takes place in late winter, since copulation appears to occur only between soft-shelled females and hard-shelled males (Watson 1972). The descent to the muddy bottoms must therefore take place

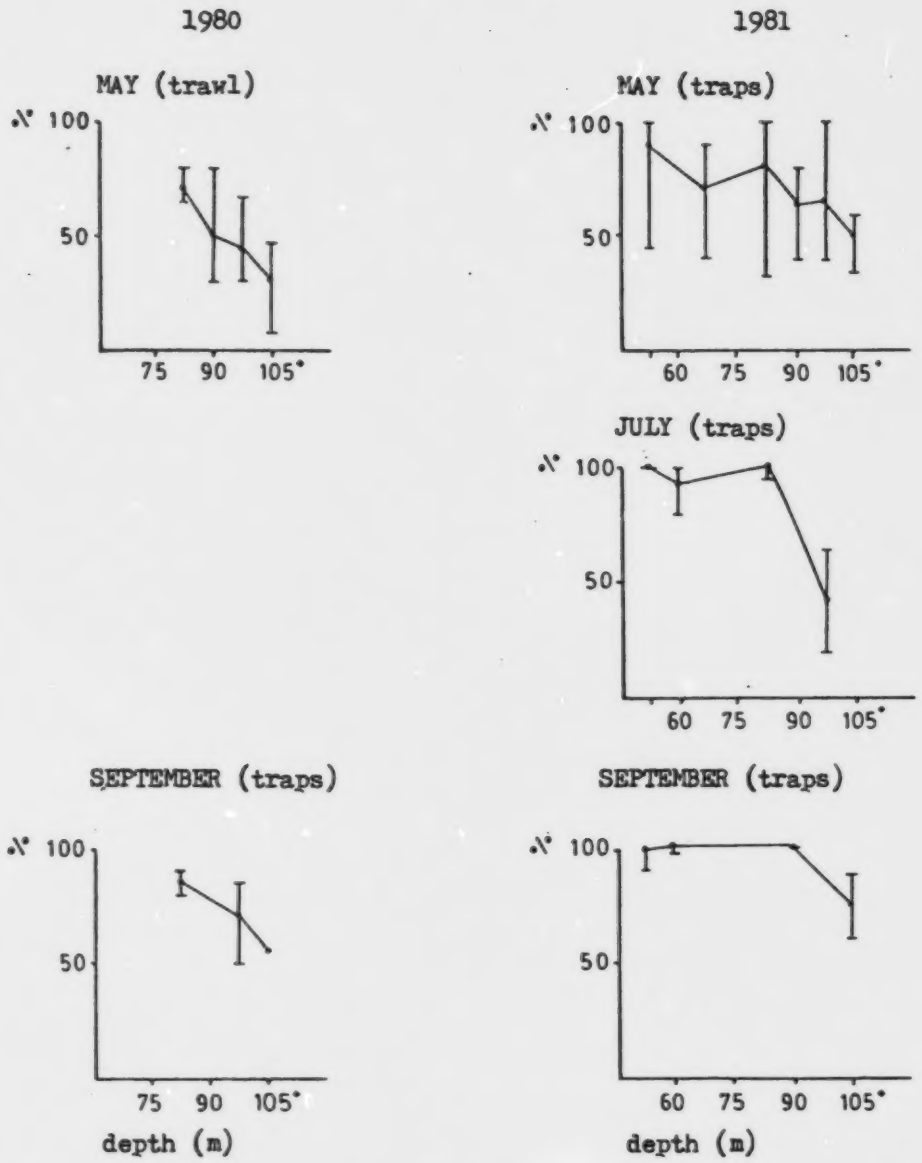

FIG 11. Variation in proportion of male crabs in samples, all regions combined; the interval indicates the extreme values observed.

during the summer, as verified by the reduction in the abundance of adult females between May and September in shallow water. The females' departure is observed in both 1980 and 1981, when it was completed by the month of

July. The male moult to maturity, in contrast, appears to occur during the summer (Watson 1969), and their descent thus cannot coincide in time with that of the females. Copulation in late winter at relatively shallow levels suggests that the adult males subsequently return from the deep water. This type of genetic migration has been observed for C. tanneri (Pereyra 1966), the males of which rejoin the females during the winter for reproduction. This hypothesis could be verified by means of more frequent sampling during the late winter.

Kon (1969, 1980) has proposed a distribution pattern for the C. opilio population in the Sea of Japan which to some extent supports that proposed here. In his opinion, the early benthic stages, which are very abundant at levels of approximately 375 m, migrate to 225 m bottoms, where the immatures are concentrated. The moult of puberty and copulation occur at this level, followed by the descent of the females to depths of 250-300 m and of the males to 325-375 m. The depths involved in the two systems, the Sea of Japan and the Gulf of St Lawrence, are extremely different, probably as a result of the hydrological conditions of the areas concerned. While our data do not permit us to hypothesize as to the location of the younger benthic stages, we do, however, note one major area of agreement, relating to the different location of the immatures and the mating zone, on the one hand, and of the adults, on the other, on the basis of a bathymetric gradient. Local conditions in the portion of the Gulf of St Lawrence studied add a granulometric element, one which appears extremely useful in this case to the spider crab.

In general, it appears that immature individuals are located primarily on heterogeneous bottoms and associated with the Macoma calcarea benthic community, and on bottoms of less than 90 m, while adults are found primarily on the deeper, muddy bottoms of the Maldane sarsi and Ophiura sarsi community. The difference in the benthic communities associated with the crab is reflected, moreover, in a modification of the diet (Brêthes et al, 1985). The observed segregation between the various elements of the population of C. opilio may be of some significance for the fishery. The sectors currently exploited are located below the 90 m level, that is, according to the proposed pattern, outside the zones in which large numbers of immature individuals occur and mating takes place. Thus, at least some of the recruitment to the fishery may originate from the higher levels unaffected by fishing operations. This recruitment mechanism, together with the selection of a trap mesh which allows females and the smaller adult males to escape, may account, at least in part, for the vigour of the stock in this region, despite a substantial increase in fishing activities over the past decade.

A number of points, however, remain unclear. It is not certain that this distribution pattern can be generalized to the entire Gulf, although increases in crab size with depth are mentioned in Newfoundland (Miller and O'Keefe 1981), and on the north shore of the Gulf of St Lawrence (Greendale and Bailey 1982; F Coulombe, P E Lafleur and J-C F Brêthes, unpublished data). Finally, the distribution of the early benthic stages and the genetic migrations of the adult males are aspects which will require further definition for a better understanding of the ecology of C. opilio.

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